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OBSERVATIONS ON THE FINE STRUCTURE OF CALLIXYLON WOOD[1]

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ABSTRACT

Secondary wood of three species of *Callixylon* of Lower Mississippian age, preserved by three different modes (fusinization, silicification, and phosphatization), have been studied and characterized in detail. Problems of interpretation at the SEM level of permineralized woods, both containing (silicified wood of *Callixylon erianum*) and essentially lacking (phosphatized wood of *C. arnoldii*) original organic cell wall material, are analyzed and discussed. In particular, it is concluded that the flat to curved surfaces showing no evidence of apertures, observed in bordered pit pairs, commonly represent pit membrane surfaces. It is accepted, however, that some concave surfaces might be the mineral accretion surfaces of incomplete pit cavity casts as proposed by Leo and Barghoorn (1976). Regions between groups of pits, previously interpreted as crassulae, may be artifacts of preservation. The fusinized wood has the general appearance of charcoal, but unlike commercially produced charcoal provides evidence of its original microfibrillar structure. The origin of fusain in the fossil record is discussed, and it is concluded that it probably had several origins, including forest fire. Since charcoal can be produced naturally in the absence of O_2 (Brown and Davis, 1973), the suggestion that fusain (charcoal) in the geologic column provides a basis for "assessing oxygen levels in paleoatmospheres" (Cope and Chaloner, 1980) is not supported. Natural sites of fusain production in the absence of O_2 are regions of vulcanism and organic sediments inhabited by anaerobic microorganisms. A circular pattern of crystal orientation in the pit borders of *C. arnoldii* is interpreted to represent the original microfibrillar pattern. Pit apertures in *C. arnoldii* are shown to be circular to slightly elliptical. Interpretive evidence of heterogeneous pit membranes in *C. arnoldii* suggests but does not prove the presence of a torus. The distinctive central region in some pit membranes of the fusinized wood of *Callixylon* sp. might represent accumulations of waste metabolites. It is argued that a torus would be highly adaptive in large pits with circular apertures.

THE IMPORTANCE of *Callixylon* lies in the fact that it encompasses anatomically preserved axes of the Paleozoic progymnosperm genus, *Archaeopteris* (Beck, 1960). *Archaeopteris* has been often suggested as representative of a group from which some early gynmosperms might have evolved (Beck, 1960, 1962a, 1966, 1971, 1976, 1981; Carluccio, Hueber and Banks, 1966; Bonamo, 1975). Consequently, *Archaeopteris* and *Callixylon* are among the most intensively studied Upper Devonian/Lower Mississippian genera. Among recent studies of *Callixylon* are those of Beck (1970, 1979). The present paper continues this series.

This investigation of tracheid morphology in *Callixylon* was stimulated by the attempt of one of us (CBB), nearly 10 years ago, to prepare a taxonomic monograph of the genus. During that study, as knowledge increased there was a corresponding decrease in ability to distinguish between previously named species. In an unpublished manuscript, four categories of species that could be easily recognized were established, but using solely secondary wood characters it was not possible to determine any objective basis upon which to decide whether these categories represented

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species or genera. The distinctive features of each of the four groups, and the considerable variation within those containing several species, suggested, however, that we might be dealing with genera rather than with species (Beck, 1969).

Among the variable characters was the tracheary pitting, including, conspicuously, the size and shape of apertures. Interestingly, however, the broad, open apertures that seemed to diverge from the more typical narrowly elliptical form were dismissed as artifactual in the belief that they had resulted from the sectioning and grinding process during slide preparation. In a more recent study employing the transmission electron microscope (TEM) to observe bordered pits in silicified *Callixylon newberryi,* Schmid (1967), utilizing a surface replica technique, showed that sectioning and grinding damage to pits can, indeed, have just such an effect (see also Beck, 1970). Observations with the scanning electron microscope (SEM), however, to be discussed in this paper, clearly demonstrate that extremes of variation in the form of pit apertures can also be a natural feature of the plant.

Schmid found no evidence of a torus in the pit membranes of *C. newberryi,* or in fusinized wood of an undetermined species of *Callixylon* (the same material as used in the present study, but observed in section with the TEM). Because, however, of the possibility that dehydration and/or degradation might have obscured evidence of such a feature, he cautiously refrained from making a dogmatic statement about its absence in these species. The present study adds some information on this subject. Another feature of interest on which this study bears is the supposed crassulae between groups of pits reported by Arnold (1929) and supported by Beck (1970). Furthermore, this study demonstrates the great utility of the SEM in studying permineralized tissues and provides an exercise in interpretation of two permineralized woods, preserved by different minerals, and which have very different appearances in SEM photographs. Finally, it provides new information about *Callixylon arnoldii* and demonstrates the preservation of the microfibrillar (or, at least, a subcellular structural) pattern in the cell walls of fusinized and mineralized woods of Lower Mississippian age.

MATERIALS AND METHODS—Three types of material were studied: 1) Secondary wood of *Callixylon* sp. preserved as fusain or semi-fusain (possibly fossil charcoal) provided by the late Professor C. A. Arnold. This wood was collected from the Berea sandstone (Kinderhookian Series) of Lower Mississippian age near Amherst, Ohio, USA. 2) Secondary wood from the type specimens of *Callixylon arnoldii* Beck (1962b) collected from the Sanderson formation of the New Albany shale, basal Lower Mississippian, near Junction City, Kentucky, USA. This wood was preserved predominantly by calcium phosphate and ferric carbonate (Scott and Jeffrey, 1914). Cell walls are heavily mineralized. 3) Secondary wood of *Callixylon erianum,* collected from the Upper Devonian Blackiston formation, New Albany shale, at Burdett Knob, Garrard County, Kentucky, USA. The wood was preserved by silicification. Cell walls are largely unmineralized.

Specimens and SEM preparations of the fusinized *Callixylon* wood are on file under number 64127, those of *C. arnoldii,* under numbers 44714 and 44715, and those of *C. erianum* under number 64128 in the Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA.

Wood of each species was broken approximately along transverse and radial planes, small pieces mounted on stubs, gold coated and observed with a JEOLCO SEM. The fusinized *Callixylon* wood was also embedded in celloidin, sectioned with a sliding microtome, and observed with the light microscope (LM).

DESCRIPTIONS—*Callixylon sp. (fusinized wood)*—The wood of this species, having been converted to fusain or semi-fusain, is in a remarkably excellent state of preservation. Indeed, one cannot distinguish macroscopically these charcoal-like specimens of *Callixylon* from the charcoal of a modern coniferophytic species. The wood is extremely light, highly friable, and nearly opaque. It has a silky, black luster and is highly reflective, transmitting light only when sectioned to a thinness of less than about 10 μm. Since bowing and fracturing of the cell walls indicate some compression of the wood, and because of its brownish translucency, it falls within the concept of semi-fusain as defined by Schopf (1948). It is also remarkably similar in appearance to the extant spruce wood subjected to high levels of gamma radiation by Antoine, Avella and Van Eyseren (1971). The means whereby or the time period over which this *Callixylon* wood was fusinized is, of course, unknown. It is probable, however, that the wood was never mineralized since there is no evidence of any residual mineral content. In preparation for sectioning with a sliding microtome, the fossil material was not even demineralized prior to embedding in cel-

oidin. Natural demineralization, possible under certain circumstances, seems most unlikely in this case. According to a letter from the personnel manager to the executive vice-president of the Cleveland Quarries Company, the specimen was "found in the middle of a block of stone measuring 6′ × 5′ × 4′2″, quarried . . . at a depth of around 60 feet at Buckeye Woods Quarry. It was discovered when workmen capped the block (split it through the middle)."

Anatomically this wood is characterized by several features of interest. The groups of bordered pits are conspicuously raised in relation to the intervening wall (Fig. 1, 2, 9), resulting largely, perhaps, from the rather expansive pit cavities of the closely approximated pit pairs (Fig. 5). The inner wall surfaces of the tracheids may have a conspicuously wrinkled appearance (Fig. 3, 4, 6, 9, 24, 26), and the pit apertures seem to be surrounded by a wide rim (Fig. 3, 4). Although these features are probably the result of shrinkage during fusinization, one clearly observes at higher magnifications a parallel (and sometimes opposing) pattern of fine striations that we believe reflect the pattern of cell wall microfibrils (Fig. 4, 24–27). The larger wrinkles and fine striations consistently form a circular pattern on pit borders (Fig. 3, 4). Between pits and on unpitted walls, they follow shallow to steep helices in what we interpret as various layers of the secondary walls (Fig. 24–27). For example, Fig. 24, the enlarged upper portion of the tracheid to the right of center in Fig. 9, illustrates a pattern of striations on the inner wall surface (arrow) following a shallow helix and deviating from the transverse by about 10°. On the inner wall surface of a contiguous tracheid (Fig. 24, double arrow), and the tracheid at the far left of Fig. 9 (Fig. 26), the striations are oriented at angles of about 15–30°, in contrast to the wrinkles which form a steep angle of about 85°. We interpret these inner wall surfaces to represent the S3 layers of the secondary walls because of the shallow helical course of the striations. The steep course of the wrinkles may very well reflect the orientation of microfibrils in the S2 layer. In some other tracheids, lacking wrinkles, the exposed surface shows a pattern of fine striations in a comparable orientation (Fig. 27, an enlarged segment of the tracheid at the far right of Fig. 9). We interpret these striations to represent the microfibril pattern in the S2 layer, exposed after the S3 layer had broken away. Figure 25 illustrates a region of the inner surface of a tracheid in contact with a ray, and forming half-bordered pit pairs with the contiguous ray parenchyma cells. A crossed pattern of striations is apparent, the angle of each helix being approximately 45–50°, but varying considerably as it passes around pits.

In some regions of this wood there is no evidence of any substructural pattern in sectional views of secondary cell walls, and the walls of contiguous cells seem to be fused together with no evidence of a middle lamella (Fig. 5, 7, 23). By contrast, however, occasionally we have observed sectional views in which some substructure is apparently preserved (Fig. 10, 25, at a).

Pit membranes are commonly in the aspirated position. When the membranes are appressed against the inner surfaces of the borders of pits being viewed in face view, the apertures appear closed (Fig. 3, 4, 9), but when appressed against the borders of the opposing pits of the pairs, the apertures appear open (Fig. 1, 2, 9). The tendency of all pit membranes in a group of bordered pit pairs to be similarly oriented is well demonstrated in a slightly oblique, sectional view (Fig. 5). The pit apertures vary in form, departing from the typical narrowly elliptical (or sometimes lenticular) configuration (Fig. 3, 4, 9, 19) to become very broad and ovoid (Fig. 6–8, 20). Pits of the latter type essentially lack pit borders. Some artifactual broadening, especially in the middle part of this range, was probably caused by checking and/or the process of fusinization (Fig. 1, 2).

The bordered pits of cross-field pit pairs—half-bordered pit pairs between tracheids and ray parenchyma cells—are also characterized by inconspicuous borders and broad apertures (Fig. 1, 9, 10, 25). At first we thought that the unusual pits with broadly ovoid apertures (Fig. 6–8) might be components of half-bordered pit pairs. Careful and extensive observations of radial sections with the LM (Fig. 20), however, have shown conclusively that they are not correlated with the positions of rays.

Another feature of at least some tracheids with such pits is the variation in pit morphology in tracheids presumably derived from the same cambial initial. Whereas one of two adjacent

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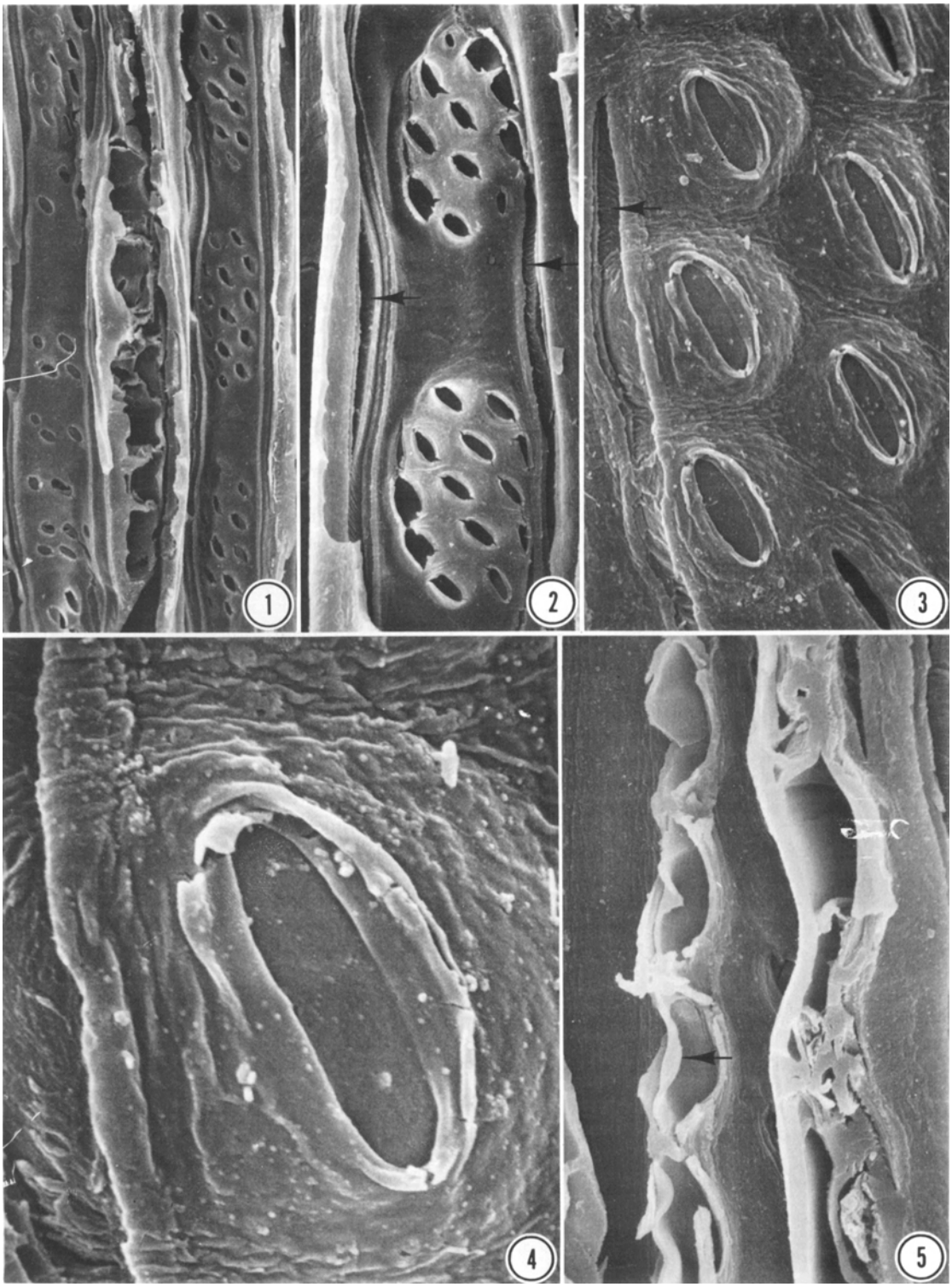
Fig. 1–5. Fusinized wood of *Callixylon* sp. **1.** Radial view illustrating grouped bordered pits (right tracheid) and cross-field pits (left) between a tracheid and ray cells. The ray (center) appears in oblique end view because the wood is badly distorted in some regions. ×550. **2.** Groups of bordered pits with elliptical apertures somewhat expanded by



checking. Splits in tracheid walls between positions of pit groups (arrows) simulate crassulae at the light microscope level. ×1,000. **3.** Bordered pits with elliptical apertures outlined by conspicuous rims. Aspirated pit membranes may be seen through apertures. Note checking in a secondary wall layer (arrow). ×3,000. **4.** A single pit from Fig. 3. Note circular pattern of wrinkles and fibril-like strands (far left); also pit membrane. ×10,000. **5.** Oblique tangential view showing pit cavities and aspirated pit membranes (arrow). Note thickness and uniformity of membranes. ×3,000.

tracheids in the same file, the radial walls of which we have photographed over their entire longitudinal extent (Fig. 6), shows pits of fairly large size, the other is characterized by great variation in size. Even the very small pits of this tracheid, however, are of the same type as the large ones, being characterized by a very narrow border (Fig. 6, 7). In this latter tracheid, the pits are clearly grouped, but rather irregularly arranged. In the other tracheid the grouping of pits is inconspicuous, or absent (Fig. 6, right), in contrast to the typical condition in *Callixylon* (Fig. 1, 2, 9). Associated with the pits are cell wall thickenings that cross the wall surface, commonly merging with or extending from the pit borders (Fig. 6, 7). These thickenings that anastomose are less conspicuous or absent between pit groups and in the central parts of tracheids.

One of the most interesting features of these pits is the pit membrane, almost completely exposed (Fig. 7, 8). The membrane of some pit pairs is characterized by a large, central circular region delimited by a narrow, enclosing ridge. The central region resembles the surface of a wool carpet whereas the surrounding part of the membrane may be slightly smoother (Fig. 8). The circular ridge delimiting the central region varies from being conspicuous to faint or absent (Fig. 7, 8). At its widest, the central region has a diameter of 6.0 μm. Pit membranes known to be characterized by the features just elucidated have not been observed in sectional view. The membranes of other pit pairs in the same wood, observed in sectional view, seem to be uniformly thick throughout (Fig. 5, arrow).

The cross-field pits (Fig. 1, lower left, 9, lower right, 10, 25) resemble those of more recent plants. The pits in the tracheid wall are essentially borderless (Fig. 10, 25). In the one region in which cross-field pits have been observed in detail, the simple pits of the half-bordered pit pairs in the ray parenchyma cell walls, extend beyond the limits of the apertures of the "bordered" pits in the tracheid wall (Fig. 10, at b).

The possibility of crassulae between the groups of bordered pits in several species of *Callixylon* (Arnold, 1929; Beck, 1970) is of considerable interest: Observations in this study suggest an alternate interpretation. The fusinized wood of *Callixylon* sp. had become badly checked at some time during or prior to the process of fossilization (Fig. 1–3). Checks appear not only as microscopic cracks extending from the ends of pit apertures, but also as more extensive longitudinal cracks (Fig. 2, 3, at arrows). Such cracks, which occur in high frequency in the walls between groups of pits (Fig. 2), could give the impression at the light microscope level of a thickened region in the wall. Indeed, our careful LM observations of radial sections of mineralized wood of *Callixylon brownii* and *C. newberryi* have revealed the same feature which strongly suggests that the crassula-like regions are simply regions between pit groups in which the radial walls of contiguous cells have separated. These regions of separation broaden as they approach the tangential walls, thus, giving the effect of crassulae between the groups of pits (Fig. 9, at arrows). The effect of crassulae is enhanced by the raised nature of the groups of pits especially when closely spaced (Fig. 9).

Callixylon arnoldii—This very distincitve species from the early Mississippian is characterized by large, predominantly uniseriate, circular bordered pits (Fig. 12, 13) arranged in radially banded groups (Beck, 1962b, fig. 2, 4). Because of the nature of preservation, bordered pits are clearly visible with the light microscope only by viewing, in unilateral incident light, radial surfaces exposed by breaking (Beck, 1962b). Consequently, previous observation did not reveal details such as the form of the pit apertures or the nature of the pit membranes.

Photographs of radial surfaces give the false impression that one is viewing only mineral casts of cell lumens and pit cavities (Fig. 12, 13). Light micrographs of both transverse and tangential sections (Beck, 1962b, fig. 1, 3) show, however, that the cell wall pattern is preserved; but the failure of this material to produce peels indicates that the walls are nearly completely mineralized. Although there is apparently little residual organic cell wall material, evidence for the presence of mineralized cell wall regions comes in addition from the crystal orientation that apparently reflects the microfibrillar pattern within the wall during the life of the plant.

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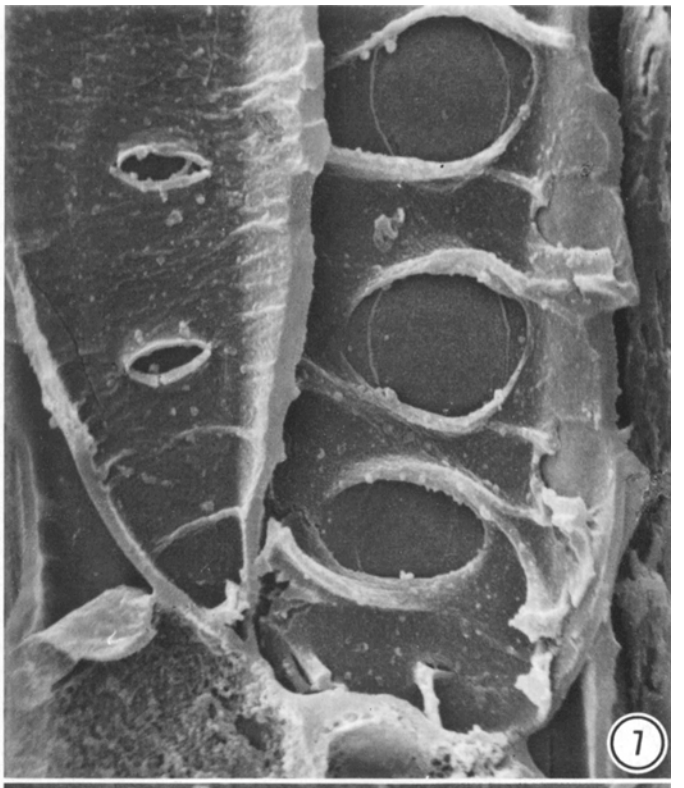
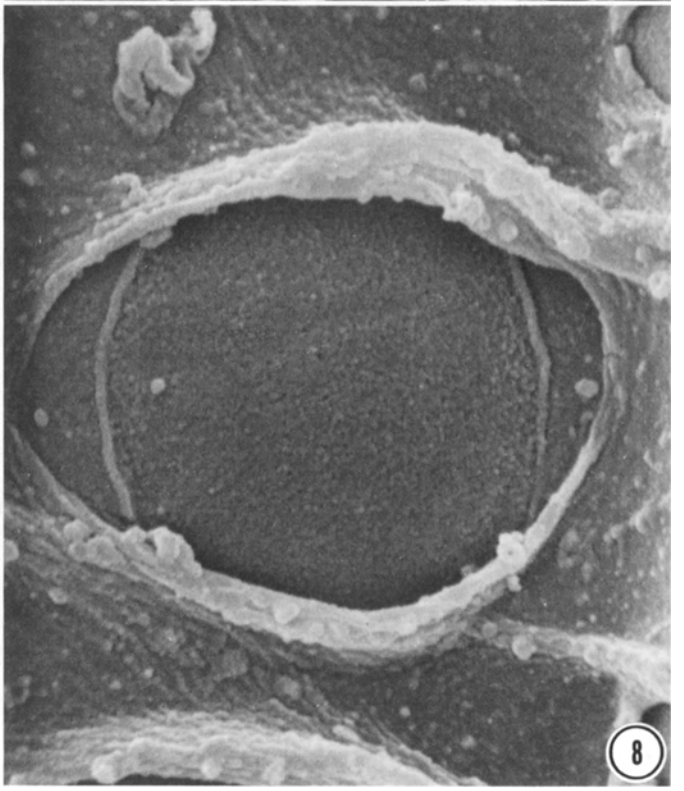
Fig. 6–8. Fusinized wood of *Callixylon* sp.; radial views. **6.** View of the inner surfaces of entire radial walls of two tracheids containing pits of unusual morphology, characterized by broad apertures (i.e., pits nearly lacking borders). See text and Fig. 7, 8 for more detail. ×500. **7.** Lower part of Fig. 6, at higher magnification, showing pits of two types in adjacent tracheid walls—small lenticular pits (left) and large pits with broadly ovoid apertures (right). Note surface wall sculpturing on both radial and tangential walls, extending, on the right tracheid, from pit borders. Also note this





feature in other parts of these tracheid walls in Fig. 6. ×3,500. **8.** Pit from Fig. 7 (right tracheid, middle) at higher magnification showing details of pit membrane. Note carpet-like texture of central region outlined by a circular rim. ×10,000.

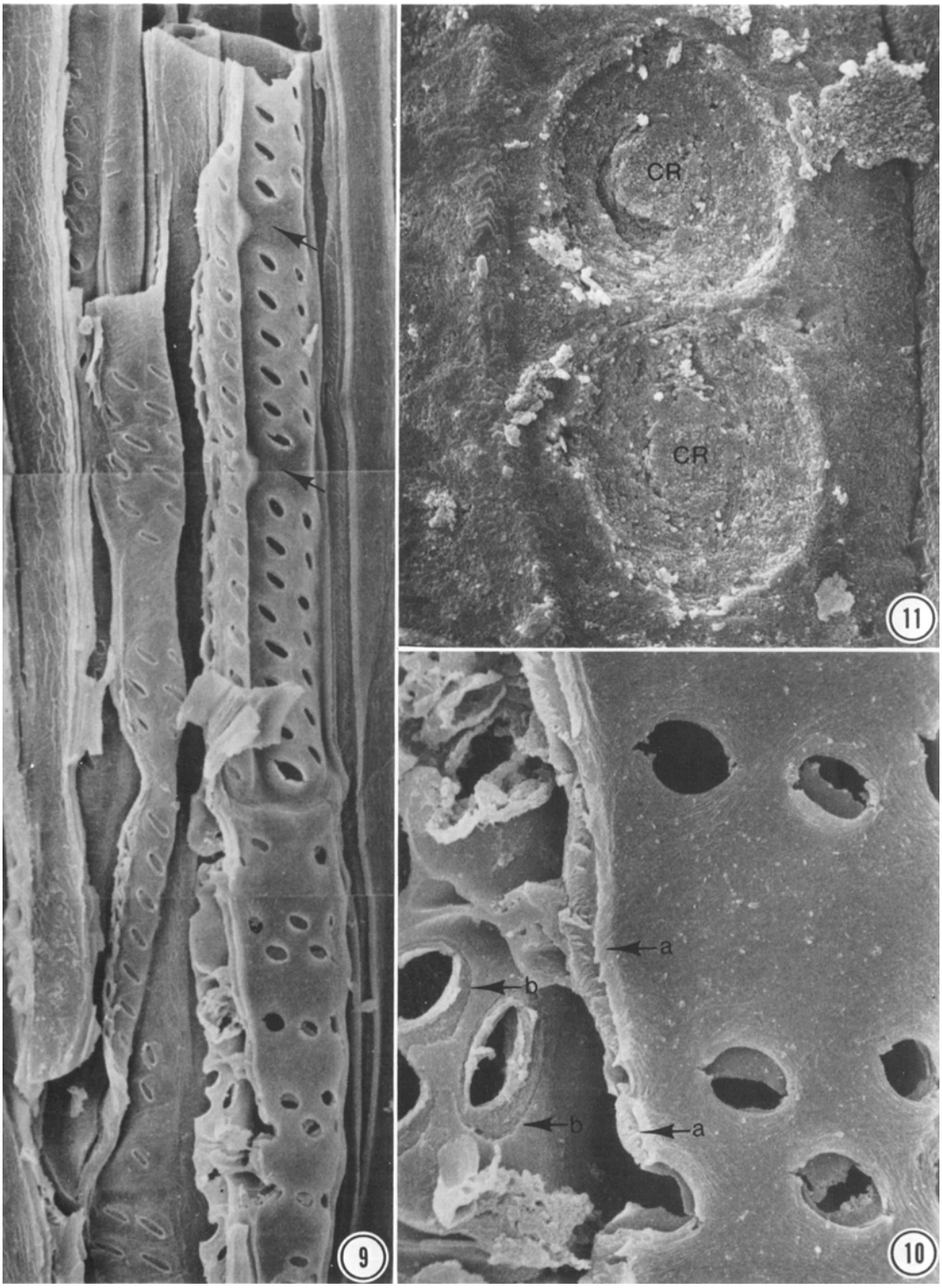


Fig. 9, 10. Fusinized wood of *Callixylon* sp. **9.** Part of a tracheid and contiguous cells. Regions between groups of pits (arrows) simulate crassulae. The expanded regions, to left of arrows, are probably the result of a separation of cell wall layers as shown in Fig. 2. Lower right region shows cross-field pits between ray cells and the contiguous tracheid. ×750. **10.** Part of Fig. 9, lower right region, at higher magnification showing cross-field (half-bordered) pit pairs from both the ray cell (left) and the tracheid (right) sides. Simple pits in walls of ray parenchyma cells are indicated

When wood of *C. arnoldii* is split radially, the breaks probably occur primarily, but not entirely, along the compound middle lamella (Fig. 33). If so, in Fig. 11–13, 15, and 16, one is viewing largely the surface of the primary walls and the S1 layer of the secondary walls. It is possible, therefore, that whether the pits are represented by mounds or by depressions often depends on the side of the pit cavity to which the pit membrane had become aspirated. It is generally accepted that most pit membranes of a particular tracheid are aspirated toward the same side of the pit cavities. It is consistent with this that the pits of a tracheid appear either predominantly (or solely) as depressions or as mounds (Fig. 12, 13). Less commonly, the pit is represented as a relatively flat circular region, which suggests that the pit membrane was in a non-aspirated position (Fig. 13, arrows, 17, lowest pit). Not uncommonly, judging from the mineral pattern, the surface of pits represented as either depressions or as mounds reflects secondary wall material (Fig. 14, 16–18). For example, in Fig. 14, 17 (two uppermost pits) and 18, some mineral representing the pit border (secondary wall) was left adhering to the primary wall or the pit cavity casts. On the other hand, Fig. 15 and 16 illustrate pits showing varying amounts of the pit membrane, and thus exposing areas of the pit border (secondary wall) of various sizes as seen from the pit cavity side. The lowermost pit (Fig. 15) shows a fragmented but the most complete, pit membrane of the three pictured, but some secondary wall (pit border) is exposed (arrows). The pit aperture cast is covered by an irregularly circular region of pit membrane in the lowermost pit, but is largely exposed in the two upper pits. In the uppermost pit of Fig. 15 (enlarged in Fig. 16), a small fragment of the pit membrane (PM) covers one edge of the aperture cast (AC) and a small part of the inner surface[3] of the pit border. Most of the inner surface of the pit broder (PB) is exposed, however, and the boundary of the pit aperture is shown in part and sharply defined. Whenever mineral representing secondary walls in the pit border is exposed, the form of the pit apertures is well-defined (Fig. 14, 16–18).

These interpretations are supported by the crystal pattern which, according to Eicke (1952, 1954, 1957) and Sen (1956, 1963) may reflect in silicified conifer wood, the original microfibrillar pattern. The consistent correlation between crystal orientation and cell wall layer or region (e.g., pit border) in *C. arnoldii* suggests that the same relationship exists in fossil wood preserved predominantly by calcium phosphate. Whenever other evidence suggests that one is viewing the surface of the primary wall, as in the region around bordered pits (Fig. 11, 14–16), the mineral orientation is largely random. This suggests that the microfibrillar orientation was essentially random, as one would expect on the basis of our knowledge of the structure of primary walls of living plants. On the other hand, in the pit borders, composed entirely of secondary wall (Fig. 14, 16–18) the crystal orientation is circular which, on the basis of extant plants, would also be expected if the crystal pattern reflects the former microfibrillar orientation.

A feature commonly observable with LM, but not previously known in *C. arnoldii*, is the pit aperture. Apertures are nearly circular to only slightly elliptical (Fig. 14–18) and measure 4.4 by 3.6 μm in mean dimensions.

The pit membrane is also of special interest. We interpret the membrane to be heterogeneous in structure, containing a central circular region, 7.1 μm in mean diameter, distinct from the peripheral region (Fig. 11, 15, lowermost pit). Although there is some evidence of a circular mineral pattern in the peripheral part of this central region, reflecting, we believe, a circular microfibrillar pattern (a condition characteristic of the torus of some living conifers—Liese, 1965), the primary evidence is the consistent circular pattern of breakage in the membrane, and the consistent diameter of this region in many pits. The ratio of the diameter of this central region to the diameter of the aperture is 1.613. This is consistent with a ratio of torus to aperture diameter of 1.574 in four species of extant conifers (3 of *Pinus*, 1 of *Pseudotsuga*) we have measured.

As in other species of *Callixylon*, the tra-

[3] In this paper, the surface of the pit border facing the pit cavity is called the inner surface, that facing the cell lumen, the outer surface.

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at arrows b. Arrows a indicate regions of cell walls in which either evidence of substructure or the distinction between cell walls of contiguous cells can be observed. ×3,000. **11.** *Callixylon arnoldii*. Radial surface of wood showing two bordered pits represented as depressions in a tracheid wall. The pit membrane, represented by the mineral layer lining each depression, consists of a central region (CR) lying over the pit aperture, and a surrounding peripheral region. The central region is defined by a circular break in the mineral layer that represents the membrane. ×2,500.

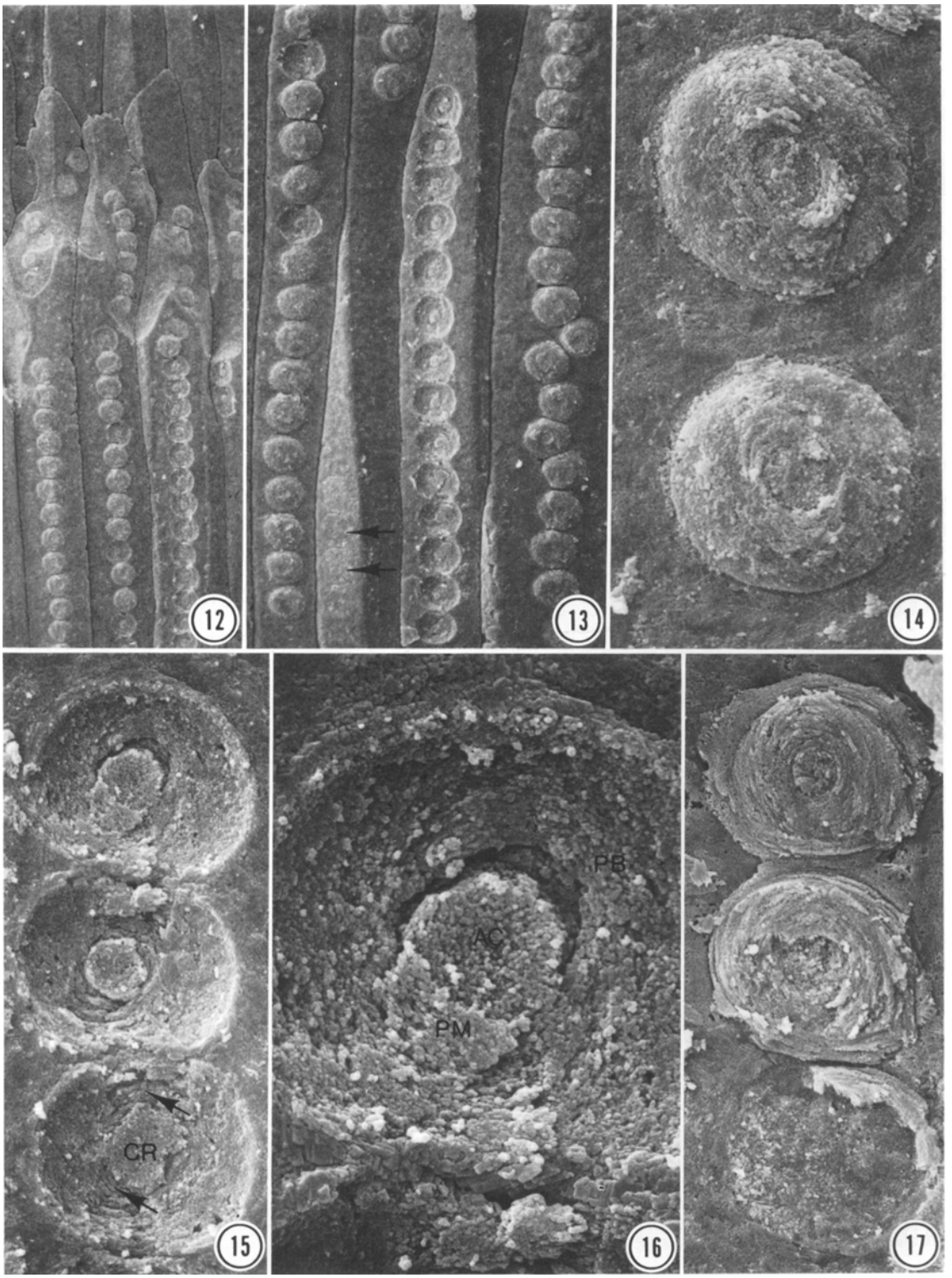

Fig. 12–17. Phosphatized *Callixylon arnoldii*; radial surfaces. **12.** Tracheid ends showing faceted tips and uniseriate circular bordered pits. ×250. **13.** Pits appear as either mounds or depressions. Note predominance of one condition or the other in a particular tracheid. This is apparently related to the fact that the pit membranes, along which breaks through pit pairs occur, are aspirated in the same direction in most or all pit pairs in the same region of a tracheid. ×400. **14.** Pits appearing as mounds illustrating the nearly circular pit apertures. Where the aperture is clearly defined, as here, some mineral representing the pit border remains. Compare with Fig. 33. ×2,500. **15.** Pits appearing as

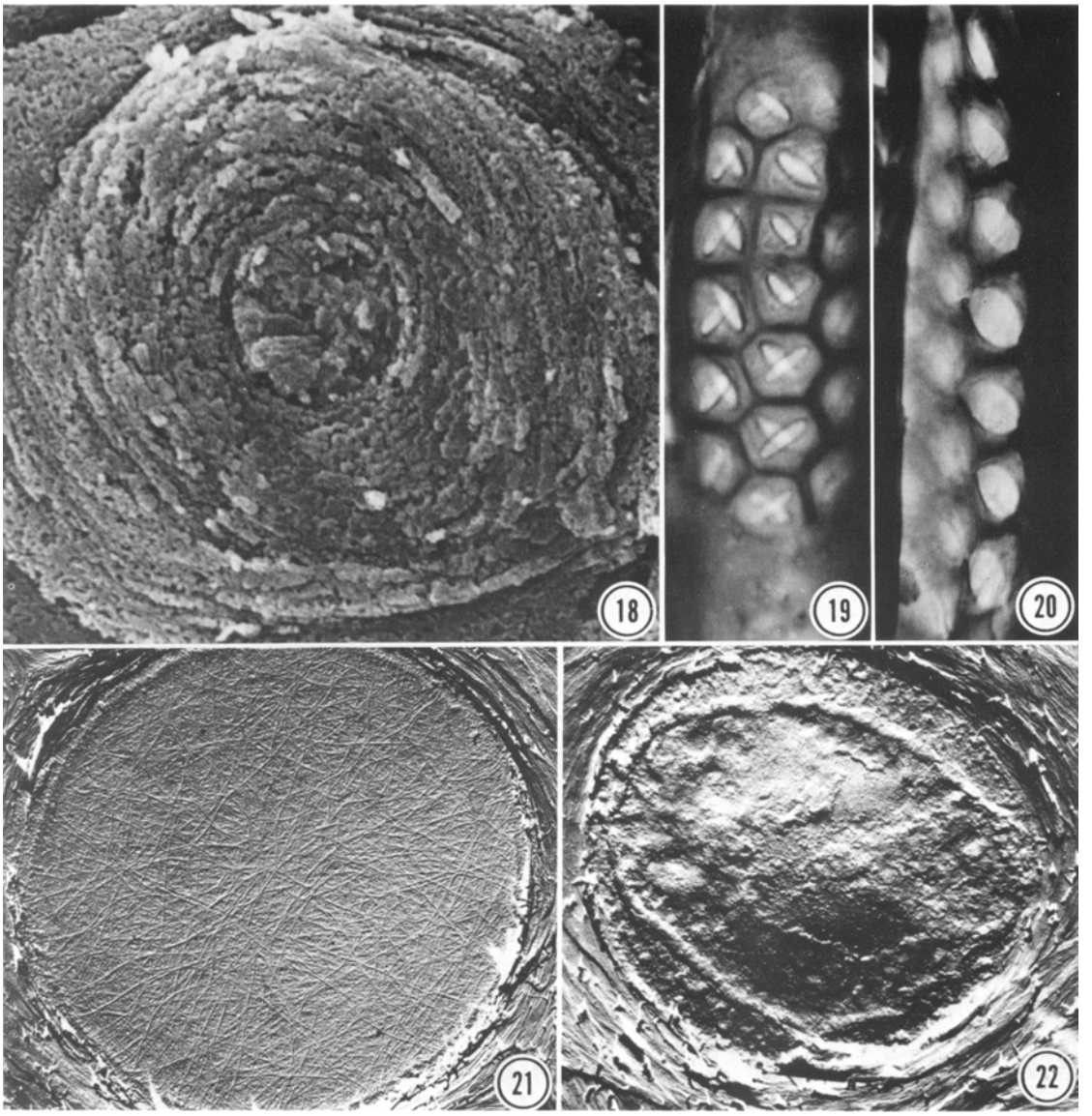

Fig. 18–20. *Callixylon* spp. **18.** *Callixylon arnoldii*. Bordered pit showing circular aperture and circular crystal pattern in pit border. ×6,500. **19.** Bordered pit pairs with typical apertures in fusinized wood of *Callixylon* sp. ×1,000. **20.** Bordered pits with broadly ovate apertures in fusinized wood of *Callixylon* sp. ×1,000. Fig. 21, 22. *Quercus falcata*; carbon replicas of membranes of pit pairs between vessel elements and tracheids (From Wheeler and Thomas, 1981). **21.** Unencrusted membrane from outermost growth layer. ×9,000. **22.** Membrane, encrusted with waste metabolites, from heartwood. ×10,000.

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depressions. In each, a mineral layer, representing various parts of the pit membrane, is present. In the lowermost pit a circular central region (CR) covering the aperture and aperture cast, is distinct from the peripheral region of the membrane, as illustrated also in Fig. 11. The inner surface of the pit border is exposed to some degree in each pit, most prominently in the uppermost pit, and in the regions indicated by arrows in the lowermost pit. ×2,000. **16.** Uppermost pit of Fig. 15 at higher magnification. Inner surface of pit border (PB) is characterized by a circular crystal pattern. Note clearly defined outline of pit aperture encircling aperture cast (AC). Aperture cast is partly covered by a remnant of the pit membrane (PM). ×5,000. **17.** Pits represented as mounds with varying amounts of the pit border intact. Uppermost pit has complete border. Note circular aperture and circular mineral pattern in border (at higher magnification in Fig. 18). Border has been almost completely broken away in lowermost pit, exposing mineral accretion surface or, possibly, the pit membrane in an unaspirated position. ×2,000.

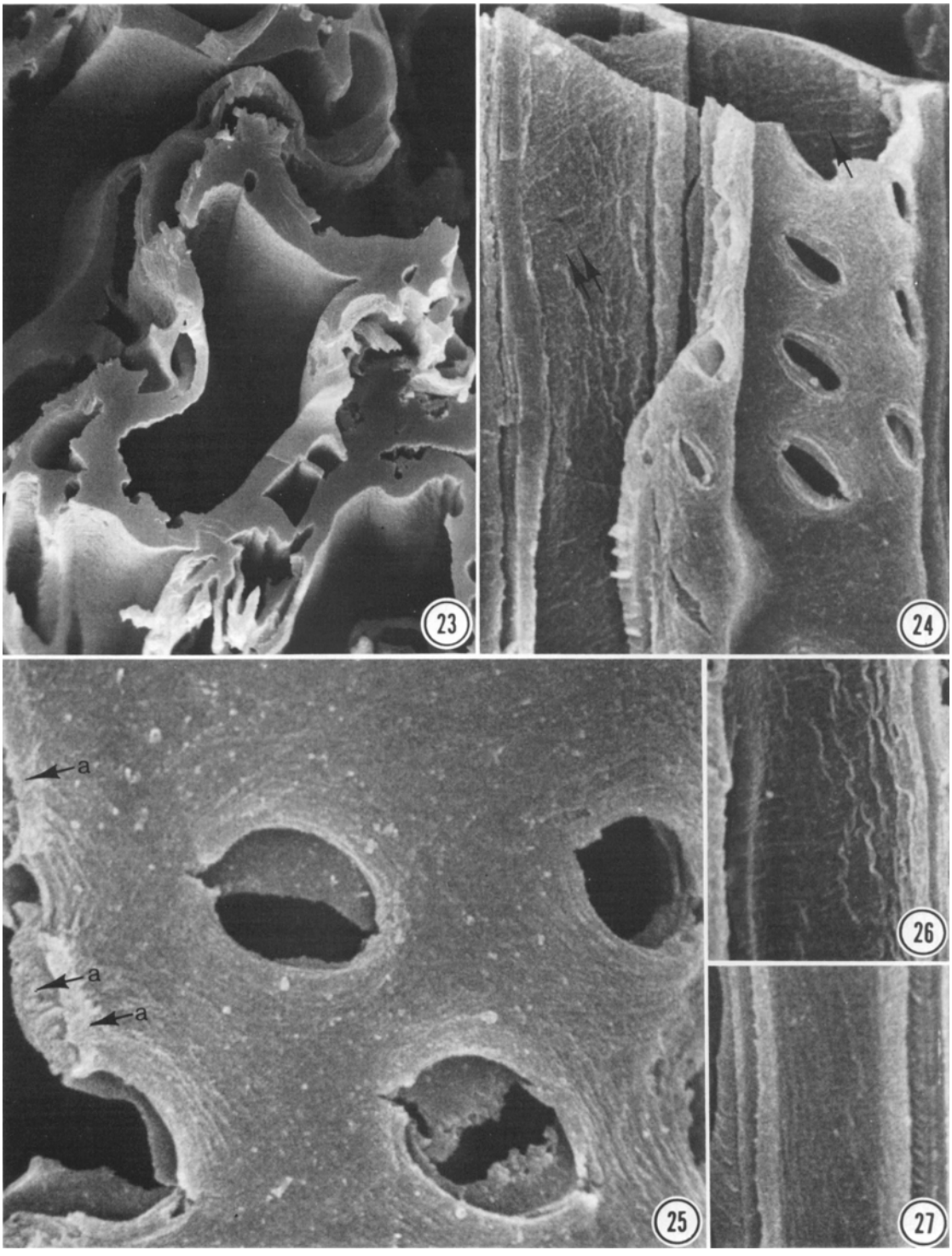

Fig. 23–27. Fusinized wood of *Callixylon* sp. **23.** Transverse view illustrating absence of visible compound middle lamella. Walls of contiguous cells are, thus, also not visible, and cell wall layers appear to be fused together. ×1,650. **24.** Enlarged upper part of tracheid and walls of contiguous tracheids shown in Fig. 9. Fine striations at angles of 10° (single arrow) and about 30° (double arrows) from transverse planes of the tracheids are interpreted to represent microfibrils or bundles of microfibrils of the S3 layers of secondary walls. Note also the pattern of steeply inclined wrinkles that may reflect the orientation of microfibrils in the S2 layer. The region between groups of pits (lower right) simulates a crassula. ×2,100. **25.** Enlargement of lower right quarter of Fig. 10, illustrating microfibril pattern on the

cheids of *C. arnoldii* are storied, but their ends, multifaceted and tapered, suggest only slight elongation and intrusive growth during development (Fig. 12).

Callixylon erianum—One of our initial objectives in choosing this wood for study was to investigate in detail the nature of the interesting ray tracheids characterized by helical wall sculpturing. Although we were unsuccessful in this regard, we observed other aspects of the wood and noted that the appearance of this silicified wood in SEM photographs is strikingly different from that of the phosphatized wood of *C. arnoldii,* thus, posing different problems of interpretation.

Unlike the wood of *C. arnoldii,* the wood of *C. erianum* is characterized by cell walls containing coalified residues of the original wall substance. This is demonstrated by the fact that this wood yields peel sections of good quality. Much, if not all, of the mineral, therefore, resides in cell lumina and pit cavities as cell lumen and pit cavity casts, and the cell wall material, of organic origin, is conspicuous in SEM photographs as a well-defined layer between pits (Fig. 28–30, arrows; compare with Fig. 33).

Because of the absence of mineral in the cell walls, radial breaks of this wood are much more irregular than in *C. arnoldii,* often exposing several different levels through a pit pair (Fig. 28–32). Furthermore, cell wall material seems, invariably, to break away from the surfaces of pit cavity casts. Whereas the pit cavity casts are, therefore, commonly exposed in face view, each providing a template (negative) replica of the inner surface of the pit border (Fig. 30, CC), the border itself has not been observed well-preserved in face view. Secondary wall typically appears only in sectional view (Fig. 28–30, arrows). Breaks that occur occasionally through and parallel to the compound middle lamella may expose mineral replicas of the surfaces of pit membranes (i.e., primary walls) (Fig. 28–32, PM). This interpretation is supported by the following analysis. Figure 30 shows three levels through pit pairs. Two pit cavity casts are shown in the center to upper right part of the photograph. The configuration and angle of the pit apertures are demonstrated on each by the broken aperture cast (AC). The angle of these apertures is opposed to that of the pit in the lower left of Fig. 30, indicating that the latter pit was in the contiguous, parallel, secondary wall of the contiguous tracheid. The essentially flat surfaces (bottom and lower right of Fig. 30), lacking any indication of pit apertures (i.e., the pit membranes), clearly lay between these secondary walls. We have not observed what we would interpret as residual organic material of the pit membranes, but believe that in many instances such flat to slightly curved surfaces (Fig. 28–32) reflect the surfaces of pit membranes that had earlier served as templates upon which mineral accretion occurred. This interpretation is further supported by the rare presence of two separate, parallel layers of mineral (A and B in Fig. 29, exposed by an unusually fortunate break) which we believe were deposited on either side of the pit membrane. The membrane is no longer visible between the layers because, as in other regions of radial surfaces, the friable organic cell wall material fell away upon breaking to expose the radial surface or was blown away during preparation for SEM observation.

In levels just below the pit membranes, one is often able to view replicas of the outer surface of the pit borders (i.e., imprints in the surface of the cell lumen casts, LC) because the pit cavity cast and enclosing secondary wall material have fallen away (Fig. 28, 29, 31, 32). In such views, the pit aperture cast is often encircled partially or completely by a furrow that is roughly parallel to the outline of the aperture (Fig. 29, 31, 32). In some other pits there is no evidence of a furrow (Fig. 18). We have no explanation for this feature. In Fig. 31, 32, we are able to view a part of a pit cavity cast (CC) and an aperture cast (AC) which attaches it to the mineral of the cell lumen tilted at an angle of about 30° from the transverse plane. The pit cavity cast, below the presumed surface of the pit membrane, has a rough appearance because it has been broken essentially in half. The pit border of secondary wall material lay in the depression around the pit aperture cast (AC, Fig. 32).

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S3 wall of region of a tracheid contiguous with a ray. Note the crossed pattern of fibrils, their deflection around pits, and the appearance of structure in sectional views of the wall (arrows a). ×6,300. **26.** Enlargement of segment of the tangential wall of tracheid at far left in Fig. 9. Note shallow inclination of fibril-like striations (15°) in presumed S3 layer, and steep inclination of wrinkles that may reflect microfibril orientation in the S2 layer. ×2,100. **27.** Enlargement of segment of the tangential wall of tracheid at far right in Fig. 9. Note steep inclination of fibril-like striations (85°) in presumed S2 layer. ×2,100.

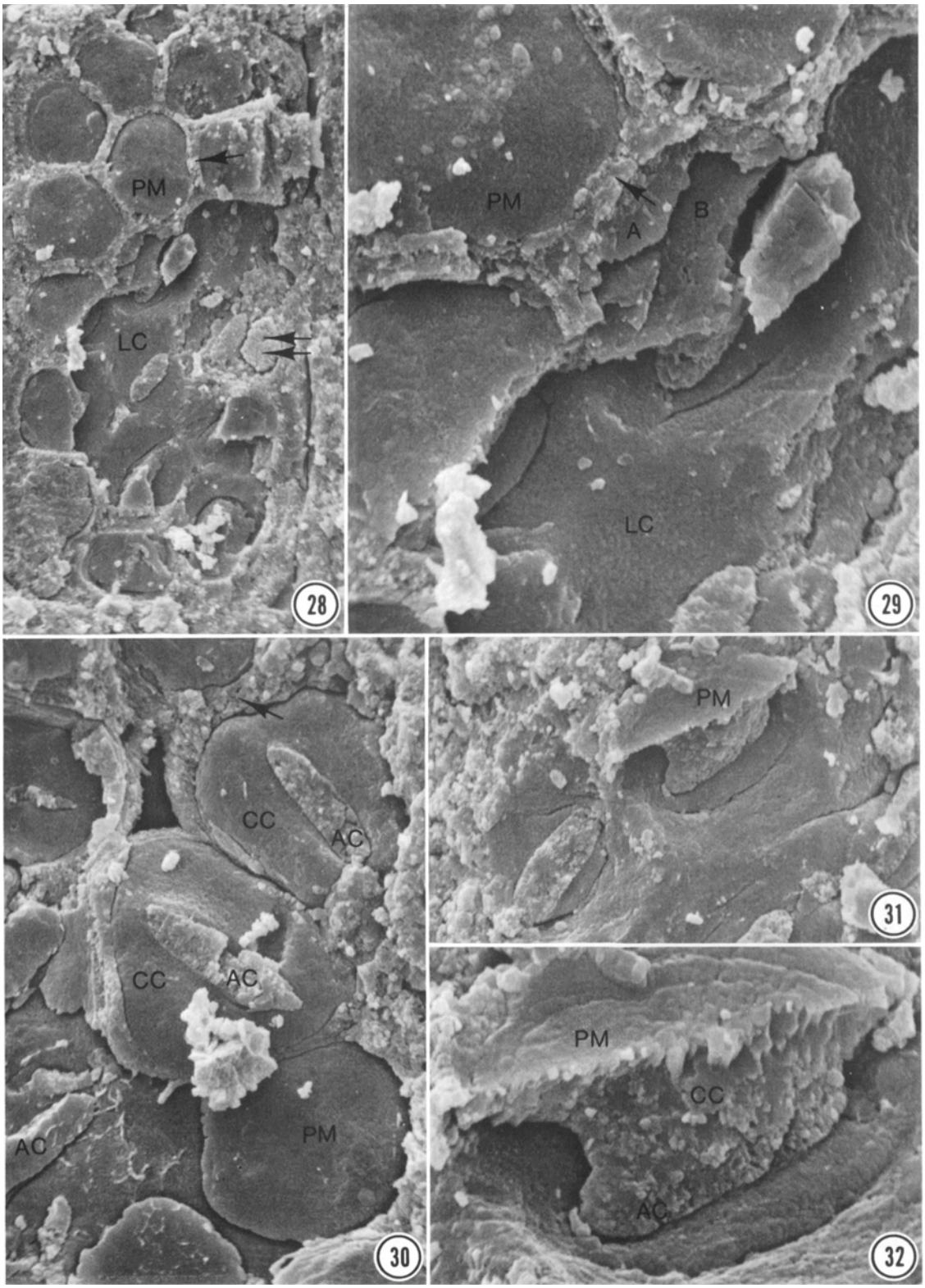

Fig. 28–32. Silicified *Callixylon erianum*; radial surfaces of wood. **28.** A group of bordered pits exposed at two levels: upper left, through the compound middle lamellae showing mineral replicas of the surfaces of pit membranes (PM) separated by organic wall material (single arrow) and lower right, at the level of the pit borders. Organic secondary

DISCUSSION—This investigation of the fine structure of the secondary wood of three species of *Callixylon* bears on several problems of rather wide interest, including the preservation of microfibrillar cell wall patterns in fossil wood, the nature and origin of unmineralized, charcoal-like fossil wood and its significance, the interpretation of the structure of permineralized wood as seen with the SEM, and the evolution of the pit membrane, including, especially, the origin of the torus. We shall discuss each of these in turn.

Cell wall microfibrillar patterns—The similarity of cell wall layering in a species of *Callixylon* to that of extant plants has been previously recorded (Schmid, 1967). Even microfibrillar patterns in cell walls have been observed in silicified or calcified fossil wood of several ages, including Tertiary conifer wood (Eicke, 1952, 1954, 1957), and the Pennsylvanian-age fern, *Psaronius* (Purelis, 1962), among others (see Sen, 1956, 1963 for references). According to Sen (1956, 1963), and essentially consistent with the views of Leo and Barghoorn (1976), Scurfield (1979) and others, surviving cellulose and/or its texture, as reflected in residual lignin, influences the orientation of crystals of the impregnating mineral which, thus, simulates the original cellulosic microfibrillar texture of the cell walls. Leo and Barghoorn (1976) propose that the process of silicification is related to the propensity of hydrogen bonding between soluble silica and the major cell wall components, cellulose and lignin.

Our *C. arnoldii* wood, as far as we can determine, provides the first evidence of microfibrillar patterns in fossil wood of Lower Mississippian age as well as in phosphatized wood. Eicke (1952) demonstrated such patterns in silicified specimens of *Glyptostroboxylon* (of Tertiary age), containing either amorphous or crystalline silica. In wood containing amorphous silica, the microfibril replicas measure approximately 250 Å in diameter, consistent with the known size of microfibrils in extant conifers. Furthermore, their parallel orientation in the wall at 40–45 degree angles between pits and in a circular pattern within pit borders is consistent with the patterns in the woods of extant species. Although not specifically stated, the components of the circular pattern, considered to reflect the microfibrillar structure of the pit borders in the wood containing crystalline silica, appear somewhat larger than in that preserved by amorphous silica. The circular crystalline pattern in the pit borders of *C. arnoldii* (Fig. 18), likewise, probably does not indicate the size of microfibrils. Nevertheless, we believe the arrangement of crystals in concentric circles, a constant feature of pits preserved as both mounds and depressions, reflects the original microfibril orientation in the pit borders.

Although the microfibrillar structure of the cell wall is reported to be destroyed by the commercial process of charcoal production (McGinnes, Kandeel and Szopa, 1971; McGinnes, Szopa and Phelps, 1974), there is good reason to believe that the microfibrillar pattern is preserved in the fusinized *Callixylon* wood. This is based on the orientation of cell wall striations. On the preserved inner surface of the radial walls of tracheids, possibly, the S3 layer, the striations occur in a crossed pattern (Fig. 25), suggesting the presence of two thin laminae in which the former microfibrils of each followed opposing helical courses at an angle to the transverse axis of the cells of about 45–50°. The striations deviate from this orientation as they pass around bordered pits. Whereas this crossed pattern may be readily visible in the vicinity of pits on the radial walls, only one helix is conspicuous on tangential walls. The low angle of the striations in the presumed S3 layer, and the deflection around pits are features characteristic of microfibril

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wall material of the borders has largely fallen away (except at double arrows). Thus, one is actually viewing the impressions of bordered pits on the surface of the cell lumen cast (LC). Compare with Fig. 33. ×1,200. **29.** Central region of Fig. 28 at higher magnification. PM, mineral replica of surface of pit membrane bounded by organic cell wall material (arrow); LC, surface of lumen cast containing imprints of pit borders. A, B, mineral layers formed on either side of the compound middle lamella. ×4,000. **30.** Pit cavity casts (CC) bearing on their surfaces elongate aperture casts (AC). Sectional view of secondary wall indicated by arrow. Aperture cast at lower left is an extension of the cell lumen cast. The opposing angles of orientation of this latter aperture cast and the two other labeled aperture casts indicate that pits in the walls of two contiguous tracheids are represented. This suggests, furthermore, that the mineral surface labeled PM lies in an intermediate level and probably represents a pit membrane. ×2,500. **31.** Surface of lumen cast from which organic wall remains have fallen away, showing an attached aperture cast broken approximately in half (and at a right angle to surface of lumen cast) showing a surface (PM) upon which the pit membrane lay. Specimen photographed at an angle of about 30° to the transverse. ×3,000. **32.** Pit cavity cast of Fig. 31 at higher magnification. PM, surface upon which pit membrane lay; CC, pit cavity cast; AC, pit aperture cast. Note furrow parallel to aperture cast. Also note such furrows in Fig. 29, 31. ×3,000.

orientation in the walls of extant plants (see, e.g., Harada, 1965a, b), as is the crossed pattern of microfibrils (Clowes and Juniper, 1968). In some other tracheid walls of *Callixylon* sp. the microfibril-like pattern follows a steep helical course of about 85°. This is consistent with the typically steep helix followed by microfibrils in the S2 layers of extant species (see Harada, 1965a; Panshin and de Zeeuw, 1980).

In some cells conspicuous wrinkles follow an identical course, presumably reflecting the pattern of microfibrils in the S2 layer. These same cells may, in addition, possess a fine, microfibril-like pattern in an orientation consistent with that of the S3 layer (Fig. 24, 26).

Pit borders in this material are often not very conspicuous in SEM photographs (Fig. 2, 9). Those observed have been characterized by a circular pattern of striations, often obscured by a parallel pattern of wrinkles, presumably the result of cell wall shrinkage (Fig. 3, 4). Although we have made a terminological distinction between wrinkles and striations, it is certainly possible that the fine fibril-like pattern may be, at least in part, a pattern of fine wrinkles. This interpretation is supported by the presence of several size classes of these features (Fig. 24–27). No matter what their size, however, we believe the wrinkles and fibril-like striations reflect the microfibrillar patterns in the several layers of the cell wall.

One should distinguish, however, between wrinkles resulting from shrinkage and the wall sculpturing in some tracheids that also seems to parallel the microfibril orientation of the S3 wall layer as, for example, in the tracheids characterized by pits with exceptionally broad apertures (Fig. 6, 7).

The substructural patterns in the cell walls in both the phosphatized *C. arnoldii* and fusinized wood of *Callixylon* sp. (this study; Schmid, 1967) are entirely consistent with those of extant plants, and lead us to conclude that the original microfibrillar structure is reflected in these fossil woods characterized by divergent modes of preservation. Eicke (1952, 1954, 1957) has observed evidence of cell wall microfibrils in silicified fossil wood, and Leo and Barghoorn (1976) suggest that fine structure details are more likely to be preserved by silicification than by other modes of permineralization. We have been unable, however, to demonstrate evidence of such structure in our silicified wood of *C. erianum*. In the absence of any apparent silica deposition in the cell walls, they fragment and fall away upon exposure of a surface by breaking, thus making direct observation of wall surfaces impossible. Judging from the surface pattern on pit membrane replicas and pit cavity mineral casts, however, both primary and secondary wall surfaces (upon which mineral accretion must have occurred) seem to have been characterized by a similar finely rugose texture (Fig. 29–32). This apparent absence on wall surfaces of any evidence of microfibrillar patterns may very well be the result of structural degradation in cell walls prior to the onset of silicification process within the wood.

The origin of fusain—Although many have suggested that fusain in the fossil record is the result of pyrolysis resulting from forest fires—indeed, that it is essentially fossil charcoal (e.g., Harris, 1958; Komarek, 1972)—the late J. M. Schopf staunchly defended the view that most fusain was probably not fossil charcoal of forest fire origin (Schopf, 1948, 1975). As stated in his own words (Schopf, 1975), "For some and probably for the majority of occurrences of fusain, the forest fire origin seems ruled out. It is unfortunate that I am not able to suggest any generally applicable, alternative explanation." Schopf's view was based largely on the absence of what he considered to be positive evidence of a forest fire origin, and the common association with fusain in coals of resinous bodies that he believed would not have been preserved had the sediment been subjected to heating (Schopf, 1948, 1975).

Recent studies of the effect of the process of charcoal formation on wood structure (Blankenhorn, Jenkins and Kline, 1972; McGinnes et al., 1971, 1974) as well as observations of charcoal-like fossil wood (Cope and Chaloner, 1980) and our observations of the fusinized wood of *Callixylon* have added new dimensions to the controversy. McGinnes et al. (1971, 1974) demonstrated that as a result of the commercial process of charcoal production during which wood is subjected to temperatures of from 470–1,330 F, there is a loss of evidence of the microfibrillar structure of the cell walls and an apparent fusion of contiguous cell walls with the consequent disappearance of the compound middle lamella. Consequently, in SEM photographs of charcoal in transverse section, the walls separating cell lumina appear as a single, homogeneous layer. Largely on the basis of this single criterion, Cope and Chaloner (1980) equate fusain in post-Devonian sediments with charcoal, and conclude that this material resulted from pyrolysis induced by forest fire.

Our detailed characterization of the fusinized *Callixylon* wood of Lower Mississippian

age suggests that this criterion might not be a sufficient basis for the conclusion made by Cope and Chaloner. Our fusinized *Callixylon*, does, indeed resemble charcoal as characterized by Blankenhorn et al. (1972) and McGinnes et al. (1971, 1974). In macroscopic features it cannot be distinguished from charcoal. Furthermore, in SEM sectional views (Fig. 5, 7, 23), its cell walls have the distinctive appearance of those of charcoal—lacking, with few exceptions (Fig. 10, 25), any evidence of the discrete walls of contiguous cells. It is of interest, however, that Schmid (1967) demonstrated the compound middle lamella, indeed, even S1 and S2 layers of the secondary walls, in TEM micrographs of ultra-thin sections of this same material. Whereas, McGinnes et al. (1971) observed that the charring process in charcoal formation led to a destruction of the "original fibrillar arrangement of the wood, resulting in a smooth amorphous-appearing wall structure as seen [with the SEM in longitudinal surface views]," the cell walls in the fusinized *Callixylon* wood, in contrast, apparently retain evidence in surface views of their original microfibrillar structure. McGinnis et al. (1971, 1974) also showed a considerable shrinkage of wood during the charcoal-forming process and concluded that the "folds" in some cells resulted therefrom. Illustrations of these folds (McGinnes et al., 1971), however, clearly demonstrate that they are different from those of the cell walls of the fusinized *Callixylon*, being smoother and more undulating and lacking any apparent relationship to the microfibrillar orientation. Another difference is the presence of microscopic checking in the fusinized *Callixylon* and its absence in the modern charcoal produced from undried wood. This difference may be of little significance, perhaps indicating only that the *Callixylon* wood was subjected to drying with resultant checking prior to the fusinization process. The fine pattern of wrinkles in the fusinized *Callixylon* that seems to reflect the microfibrillar orientation might also have resulted from drying prior to fusinization, although we are not aware of a comparable pattern in extant woods that had dried prior to sectioning. Without doubt, the most significant difference between the fusinized wood of *Callixylon* and modern charcoal is the presence of the microfibrillar pattern in the *Callixylon* wood.

There is extensive evidence that thermal degradation of cellulose occurs between about 250 and 350 C (see Beall and Eickner, 1970). It is not surprising, therefore, that pyrolysis at temperatures above about 300 C (Cope and Chaloner, 1980) destroys evidence in SEM photographs of the microfibrillar structure of the walls. For these reasons one is led to hypothesize that fusinization of the *Callixylon* wood occurred either at lower temperatures or by a different process. The first of these hypotheses is consistent with the observations of Kollmann and Sachs (1967) that in wood subjected to temperatures up to 240 C in the absence of oxygen for 2½ hours, the microfibrillar structure in the wood of both angiospermous and coniferous species is not visibly modified. According to Browne (1958), combustion of wood usually does not occur below a temperature of about 280 C. Consequently, there is some doubt that our *Callixylon* wood was fusinized during a forest fire since temperatures at or above ground level in such a conflagration commonly exceed 300 C (Brown and Davis, 1973). This is true also of smouldering peat fires in which temperatures greatly exceed the combustion level of wood, but in which combustion may be restricted by low levels of O_2.

The conclusion that our fusinized *Callixylon* may not have had a forest fire origin is based on current knowledge of the structure of charcoal produced by a commercial process at high temperatures in the absence of oxygen, and on the assumption that comparable temperatures, or at least temperatures above 300 C, characterize conditions during forest fires in which natural charcoal is formed. Unfortunately, we know almost nothing about the range of conditions under which natural charcoal is formed. Equally important, as far as we know, nothing is known about the variation in fine structure of natural charcoal. Nevertheless, we have some doubt that *all* fusain is natural charcoal, and serious reservations about the view that all fusain in the fossil record has had a forest fire origin. Consequently, we are not convinced that the presence of fusain (or charcoal?) in the geologic column can safely be used as an indicator of the level of atmospheric oxygen as proposed by Cope and Chaloner (1980). As noted by Brown and Davis (1973, p. 156), charcoal may be formed under natural conditions in the absence of O_2. They state, "If the wood specimen is well insulated, the temperature rise from pyrolysis will, in turn, increase the reaction rate and hence the rate of heat release. The accelerating rise of temperature continues until the volatile material ignites spontaneously [if O_2 is available] or is distilled off and charcoal remains." Such conditions must have developed frequently throughout geologic time from the early Pa-

leozoic onward as the result, almost certainly, of volcanic activity and, possibly, of the respiration of microorganisms in organic sediments.

Interpretation of permineralized wood structure—In both of the permineralized woods (*C. arnoldii* and *C. erianum*) in this study, radial breaks exposed flat to slightly curved surfaces in bordered pit pairs. We have interpreted these surfaces, lacking any evidence of apertures, as representing pit membranes in the unaspirated position. Comparable surfaces have been similarly interpreted by other workers (e.g., Schmid, 1967; Grierson, 1976; Stein, 1981) in other material. From their studies on silicification, Leo and Barghoorn (1976) developed a model which would seem to provide, at least in part, a rational alternative explanation for the structural appearance of some permineralized secondary wood. Their experimental studies of silicification suggest that silica deposition begins first on surfaces at the periphery of cavities such as cell lumina and pit-pair cavities, and proceeds toward the center of the cavities.[4] Often, however, according to Leo and Barghoorn (1976), the process of silica accretion may be incomplete, leaving an unfilled region in the center of the pit cavity. They suggest that such regions would form planes of weakness through pit pairs. Consequently, in radial breaks of silicified woods these concave halves of pit-pair cavity casts would be exposed in face view. Since mineralization of the phosphatized fossils from the New Albany shale seems to follow a pattern similar to that described by Leo and Barghoorn (1976) for the silicification process, it is possible that in both the phosphatized *C. arnoldii* and the silicified *C. erianum,* at least some of the flat to slightly curved surfaces in pit pairs that we have interpreted as pit membrane surfaces (Fig. 13, 17, 28–32) might represent mineral accretion surfaces. We are not convinced, however, that this intepretation applies validly to all, or even to many, such surfaces in this or other fossil material for the following reasons.

Leo and Barghoorn (1976) dismiss the pit membrane (or, as they state, "the torus") as "not critical" and omit it from their diagrams and, as far as we can tell, from their analysis. Since they emphasize the deposition of silica on wall surfaces, they apparently assume, but do not so state, that the pit membrane is in an aspirated condition in fossil wood. They are, thus, free to consider silica deposition in a single cavity per pit pair. Of course, when the pit membrane is in the unaspirated position there are two cavities per pit pair, one on either side of the membrane.

Detailed studies by several workers on aspiration of pit membranes in members of the Pinaceae are pertinent to this problem. Phillips (1933) showed that upon drying aspiration occurs in nearly all pits in early-wood tracheids, but over 30% of the pits in late-wood tracheids remain unaspirated. He believed that aspiration was caused largely by surface tension which pulled the pit membranes to one side as water evaporated from the pit cavities. These ideas have been supported and expanded by Liese and Bauch (1967), Hart and Thomas (1967), Comstock and Côté (1968), Thomas and Kringstad (1971), Fengel (1972) and Petty (1972). Petty determined that during aspiration in early wood the pit membranes would be stretched beyond their capacity to rebound to their original positions, but he agreed with Comstock and Côté (1968) and Thomas and Kringstad (1971) that aspiration would be permanent only upon chemical bonding between the membrane and the inner surface of the pit border. Because of the greater displacement of the membranes required to accomplish aspiration in pit pairs of late-wood tracheids, Petty determined that aspiration in some of the late wood would not occur since the surface tension force would not be great enough to counter the mechanical resistance of the membrane.

Unfortunately, there seems to be little information on the behavior of pit membranes in extant pteridophytes or gymnospermous plants lacking a torus. It would appear from the work of both Hart and Thomas (1967) and Petty (1972), however, that the torus per se would not be significant in the aspiration process, since whether or not displacement of the membrane takes place is apparently related largely to the distance between the membrane and the pit border (i.e., the depth of the pit cavity) and the ability of the membrane to resist the surface tension force of water as it evaporates.

It is important to observe that Liese and Bauch (1967) demonstrated that the relatively primitive type of pit membrane in *Thuja,* lacking a well-defined torus and often lacking a highly perforate margo, requires greater surface tension to effect aspiration than the typical pinaceous type. Because the pit membrane of *Callixylon* sp. seems to be a rather sturdy complex of wall layers (Fig. 5), probably lacking the fragile peripheral margo structure of pit

[4] This view contrasts with that of Scurfield (1979) who believes initial silicification begins *within* the cell walls.

membranes in the Pinaceae, it seems likely that mineral would have been deposited on both surfaces of this membrane when in the unaspirated position. Furthermore, even under conditions of drying it is probable that the pit membranes in many cells maintained their unaspirated positions. Even in those that became aspirated, however, because of the considerable thickness of the membranes in at least some species of *Callixylon* (Fig. 5; see also Schmid, 1967, fig. 3), there is every reason to believe the radial plane of weakness would commonly run through the compound middle lamella (Fig. 33), thus revealing in permineralized woods the pit membranes in surface view as in Fig. 11, 15–17, 28–32.

Thus, while the model of Leo and Barghoorn (1976) may very well apply validly to some permineralized woods or some parts of permineralized woods, we emphasize strongly the probability that the surfaces (as in our Fig. 11, 15–17, 28–32) within pit pairs, whether flat, concave or convex, do, indeed, commonly represent pit membranes and we believe that the similar interpretations of other workers (see above) are, likewise, correct.

Evolution of the pit membrane—The evolution of the pit membrane has long been a problem of wide interest. Schmid (1967) found no evidence for a torus in the pit membranes of *Callixylon* sp. and *C. newberryi* or *Cordaites ?iowensis*, and observed that the torus is not reported to appear in the geologic record until the Jurassic when it is characteristic of conifers such as *Metacedroxylon*, *Protopiceoxylon* and *Xenoxylon* (Table 1). Schmid (1967) supported the viewpoint of Eicke (1958a, b) that the primitive type of pit membrane in gymnosperms was probably homogeneous, consisting of randomly arranged microfibrils much like that of *Cycas*. The highly specialized pit membrane of the Pinaceae with its central torus, lenticular in section, and highly porous peripheral margo of radiating strands is clearly advanced. Krahmer and Côté (1963), Liese and Bauch (1967) and Schmid (1967) suggested that the type of pit membrane characteristic of *Thuja* and *Thujopsis* represents an intermediate condition. According to Liese and Bauch (1967) the pit membrane of these genera lacks a torus, but has a peripheral region of tightly packed, radiating, microfibrillar strands among which are small open spaces. Eicke (1958a, b) and Liese (1965) considered the *Araucaria* pit membrane to be very similar to the thujoid type except that a central accumulation of matrix material stimulates a torus. More recently, Bauch, Liese and Schultze (1972) surveyed the bordered pits of 120 species of 47 genera of gymnosperms and modified Liese's 1965 classification of gymnospermous pit membranes into six new types. *Araucaria* and *Thuja* were regarded in the 1972 paper to have essentially identical pit membranes containing a dense central region (defined as a torus) exhibiting a "flat transition into margo without essential difference in thickness."

Our observations and interpretations of fusinized and permineralized *Callixylon* woods suggest that the pit membranes of at least some Lower Mississippian plants were more structurally complex than has been suspected heretofore.

The central region outlined by a ridge of material that characterizes the pit membranes in the fusinized *Callixylon* (Fig. 7, 8) provides what might appear to be the most conspicuous evidence of possible membrane heterogeneity. We cannot, however, state with any confidence that this central region represents a torus, or even an intermediate condition in the evolution of the torus. Indeed, because this feature was not observed by Schmid (1967) in his TEM study of fusinized *Callixylon* sp., and because we did not observe it extensively in this study, we propose an alternative explanation, suggested by Dr. Elisabeth Wheeler. Waste metabolites often accumulate on pit membranes, especially in heartwood of angiosperms (see, e.g., Thomas, 1976). Angiospermous pit membranes are characterized by randomly dispersed microfibrils which may be clearly demonstrated in intervessel pit pairs in sapwood (Fig. 21). In heartwood, these membranes often become encrusted by centrally located waste metabolites, simulating a torus (Fig. 22). The similarity of such an encrustation, especially, the enclosing rim on the red oak membrane (Fig. 22), to the central region of some of the pit membranes in our fusinized *Callixylon* (Fig. 8) is apparent. Thus we have two interpretational options. Although we are unable at present to make a definitive choice, we favor the possibility that the rim-enclosed, central region of the membranes in some pits of our fusinized *Callixylon* sp. represents an encrustation of metabolites.

The evidence for possible heterogeneity in the pit membranes of *C. arnoldii* is of a different nature. The very common and repeated occurrence of a circular break in the mineral layer that we interpret as the pit membrane (Fig. 11, 15) suggests its possible differentiation into central circular and peripheral regions. The fact that these circular regions are constant in size and position, and that the size

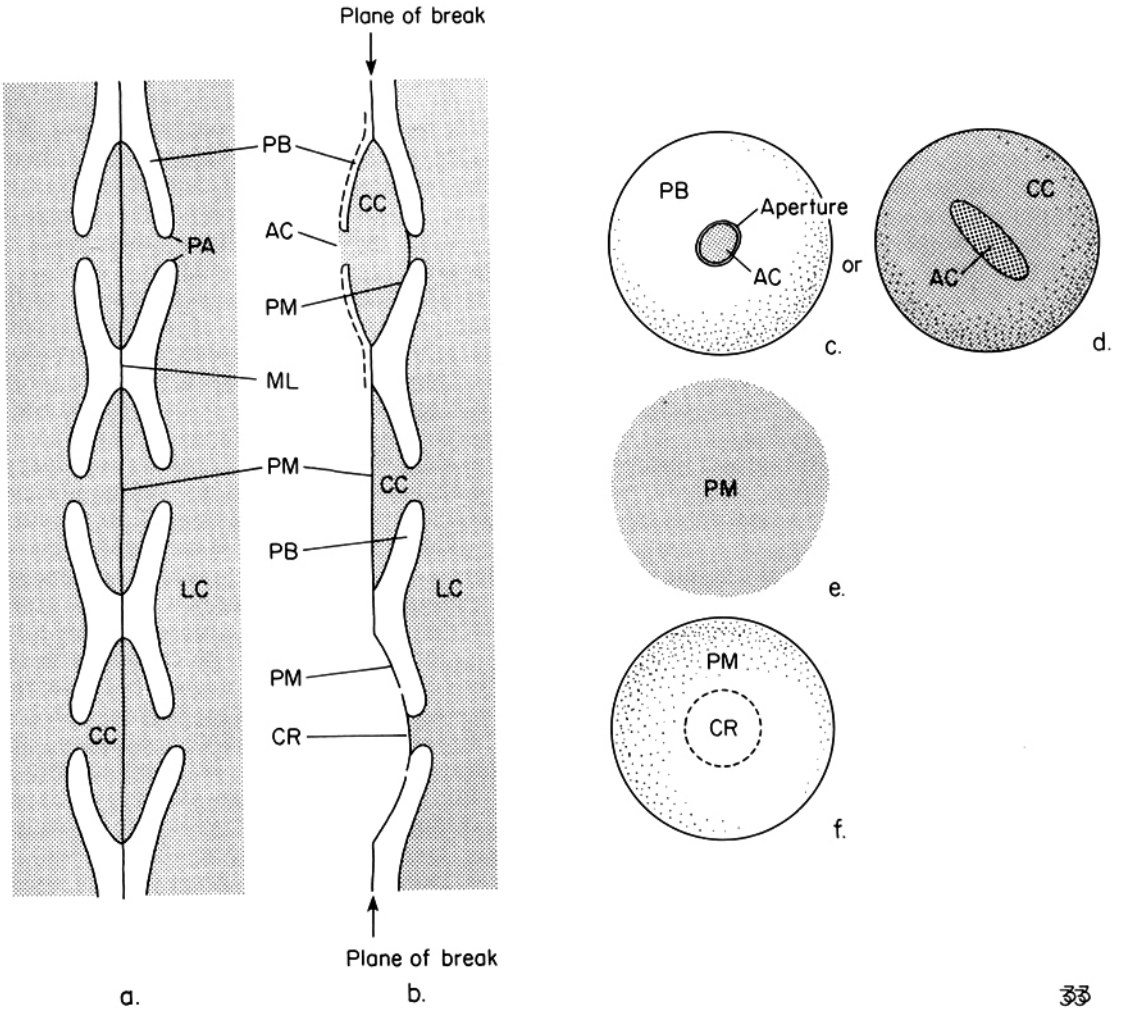

Fig. 33a–f. Interpretive drawings of permineralized secondary wood of *Callixylon*, illustrating features of both *C. arnoldii* and *C. erianum* as seen in SEM photographs. AC = aperture cast (shaded), CC = pit cavity cast (shaded), CR = central circular region of pit membrane, LC = cell lumen cast (shaded), ML = compound middle lamella, PA = pit aperture, PB = pit border, PM = pit membrane or its surface replica. **a.** Sectional view of contiguous tracheid walls containing bordered pit pairs with unaspirated pit membranes. **b.** Sectional view of contiguous tracheid walls illustrating variation in the plane of a radial break through bordered pit pairs. **c.** In the uppermost pit pair, shown in face view as observed from the left, some of the pit border has persisted (following the break). Its thickness is variable and unknown, thus it is indicated with a dashed line. The pit aperture is distinct in face view (c) and encloses an aperture cast. The pit membrane is shown aspirated to the side opposite the viewer (33b, uppermost pit pair). If the membrane were aspirated to the viewer side, the appearance in face view would be the same unless the aperture cast had fallen out of the aperture. In that event, one would observe the surface of the pit membrane within the aperture. The face view in 33c represents a common condition in *Callixylon arnoldii*. **d.** When the organic remains of the pit border fall away, upon breaking the wood, as in *C. erianum*, the pit cavity cast is exposed as in 33d. The surface of this pit cavity cast is a replica of the inner surface of the pit border. An aperture cast is also conspicuous. **e.** If the plane of the break follows the pit membrane when it is in an unaspirated position (33b, center), one observes an essentially flat to somewhat curved surface replica of the pit membrane in face view (33e). If the pit membrane has been mineralized, the surface material may represent the original membrane. If the plane of the break follows the pit membrane when it is in an aspirated position away from the viewer (when viewed from the left) (33b, lowest pit), a face view may show the essentially intact membrane (33f) or fragments of it of various sizes, and regions of the inner surface of the pit border below (Fig. 15, 16). This will be true in a wood in which permineralization is complete, including the cell walls, as in *Callixylon arnoldii*. **f.** In 33f, a mineralized pit membrane of *C. arnoldii* is illustrated with its characteristic circular central region. In a wood like *C. erianum*, however, in which cell walls are unmineralized, a radial break which excludes the pit cavity cast, as in the lowest pit of 33b, usually reveals the surface of the cell lumen cast because the friable organic remains of the pit border commonly fall away. The surface of the lumen cast thus contains a replica of the outer surface of the pit border surrounding the pit aperture cast (see Fig. 28, 29, 31, 32).

TABLE 1. *Nature of pit membranes versus shape of pit apertures in selected fossil woods*

Taxon	Mode of investigation (reference)	Nature of pit membrane	Shape of pit apertures
UPPER DEVONIAN			
Callixylon erianum	LM and SEM (this study)	Homogeneous, no torus	Narrow, slit-like
Callixylon newberryi	LM and TEM, replicas (Schmid, 1967)	Homogeneous, no torus	Narrow, slit-like
LOWER MISSISSIPPIAN			
Callixylon arnoldii	LM and SEM (this study)	Heterogeneous, possible torus or torus precursor	Circular to only slightly elliptical[a]
Callixylon sp. (fusinized material)	LM and SEM (this study) LM and TEM, thin sections (Schmid, 1967)	Homogeneous, no torus to ?heterogeneous	Variable, very broad and ovoid to usually narrowly elliptical (or sometimes lenticular)
PENNSYLVANIAN[b]			
Cordaites ?iowensis	TEM, replicas (Schmid, 1967)	Homogeneous, no torus[c]	Narrow, slit-like
PERMIAN[b]			
TRIASSIC[b]			
JURASSIC[d]			
Metacedroxylon scoticum[e]	LM (Holden, 1915)	Heterogeneous, distinct torus	Circular
Protopiceoxylon wordii	LM (Walton, 1927)	Heterogeneous, distinct torus	Circular
Xenoxylon latiporosum	LM (Watari, 1960)	Heterogeneous, distinct torus	Circular to elliptical
CRETACEOUS			
8 conifer species listed in Schmid (1967)	LM	Heterogeneous, distinct torus	Circular *or* circular to elliptical and lenticular
TERTIARY			
2 *Abietoxylon* species	LM (Roy and Hills, 1972)	Heterogeneous, distinct torus	Elliptical
Glyptostroboxylon sp.	LM and TEM, replicas (Eicke, 1952, 1954, 1957)	Heterogeneous, distinct torus	Circular
2 other conifer species listed in Schmid (1967)	LM	Heterogeneous, distinct torus	Circular
23 conifer species	LM (van der Burgh, 1973)	Heterogeneous, distinct torus	Circular *or* circular to elliptical

[a] This is the earliest known woody plant with bordered pits characterized by circular pit apertures.

[b] We are aware of no LM reports of Pennsylvanian, Permian, or Triassic tori. Critical SEM or TEM studies of wood of these ages are urgently needed.

[c] Thomson (1914) was unable to detect tori in any cordaitean wood and concluded that they were absent in the Cordaitales.

[d] These are the only Jurassic records of tori of which we are aware.

[e] This species is variously placed in *Metacedroxylon*, *Protocedroxylon*, *Araucariopitys*, or *Embergerixylon* (Lemoigne, 1970).

ratio between them and the circular pit apertures is similar to that of some modern conifers characterized by tori and circular pit apertures, supports this argument. It should be noted further that the presence of a torus in a tracheid with pits characterized by circular apertures, as in the Pinaceae, might be more highly adaptive than in one with slit-like apertures characteristic of some other gymnosperms. It is known, for example, that under conditions of water stress the pressure gradient between an aspirated and an unaspirated cell is greater than when soil water supply is adequate (Conrad Yocum, pers. commun., 1980). Consequently, the pit membrane has to be strong enough to resist such a pressure gradient when aspirated,

and yet porous enough to allow efficient water movement across it when unaspirated. Thus, the torus and margo have evolved—the torus adapted for withstanding large pressure gradients, the margo for efficient water transport across the membrane. We suggest that among progymnosperms and gymnosperms with conifer-like pits, the membrane with a torus is apparently highly adaptive in large pits with circular apertures since it would be less likely to rupture than a homogeneous membrane of uniform thickness and porosity. It could also provide effective valve action in such a pit. In a pit with slit-like apertures, a membrane containing a torus and a highly perforate margo might, indeed, be nonadaptive since, as suggested by Bailey (1958), it would be characterized by "defective valve action." That is, it would be ineffective in closing the pit aperture. By contrast, a less specialized, homogeneous membrane would probably be adaptive in pits with slit-like apertures. One would predict therefore, that the primitive pit membrane would be homogeneous in structure, the entire membrane serving the dual functions of mechanical resistance to hydraulic pressure and efficient water transport.

These views are consistent with the fact that extant gymnosperms that lack tori are characterized by slit-like pit apertures as, for example, the Cyadaceae, *Gnetum* and *Welwitschia*. Those whose pit membranes are not clearly differentiated into torus and margo (or are considered structurally intermediate) are characterized by a mixture of aperture types including slit-like, narrowly elliptical, and oval to circular, as in the Araucariaceae and Taxodiaceae (see, e.g., Greguss, 1955, 1968, 1972; Eicke, 1958a, b; Liese, 1965; Bauch et al., 1972). On the other hand, those extant gymnosperms characterized by well-defined tori such as Pinaceae, Cephalotaxaceae, *Ephedra* and many Cupressaceae and Podocarpaceae (Bauch et al., 1972) characteristically have circular to only slightly elliptical apertures.

This correlation of pit membranes containing a torus with circular pit apertures applies, as well, to all fossil gymnosperms for which the relevant data are available (Table 1). We suggest that it may apply to the progymnosperm, *Callixylon*, as well (Table 1). This study, and that of Schmid (1967), show that of the four species of *Callixylon* whose pit structure has been carefully studied, *C. newberryi* (Schmid, 1967) and *C. erianum* are characterized by homogeneous pit membranes and slit-like or narrowly elliptical apertures. The fusinized *Callixylon* sp. with predominantly narrowly elliptical pit apertures may also have a homogeneous pit membrane, although, as we have already indicated, some pit membranes exhibit an appearance of structural heterogeneity as observed with the SEM. We have however, interpreted this appearance to reflect an accumulation of waste metabolites on the membrane.

The only known species of *Callixylon* with circular pit apertures, *C. arnoldii*, provides the best evidence of a heterogeneous membrane. Although the correlation of torus and circular pit apertures seems to characterize gymnosperms, it should be noted, in the words of Wright (1928), that "the presence of a round pore [i.e., a circular aperture] does not necessarily entail the development of a torus." Angiosperms, of course, are characterized predominantly by more or less circular pit apertures, but universally lack tori. Clearly, therefore, factors other than aperture shape must have been relevant for the evolution of the torus, and one such factor certainly must have been size of the pit, as suggested long ago by Jeffrey (1917) and Wright (1928). As Jeffrey (1917) noted, pits with tori tend to be larger than those without tori. This correlation seems to characterize the gymnosperms.[5] In addition, as is well known, intervessel pits of angiosperms are appreciably smaller on the average than intertracheary pits of gymnosperms.

The corollary of tori occurring in larger pits as an adaptation preventing rupture of the pit membrane would seem to be that pit membrane deflection in smaller pits need not be disruptive of the pit membrane since the pit borders would apparently be sufficiently supportive of the pit membrane (see Thomas, 1972). In certain angiosperm families characterized by vestured pits, the vestures would presumably support the membranes and, thus, prevent rupture during pressure drops (Zweypfenning, 1978), even in relatively large pits.

It is, perhaps, significant, therefore, that the pits of *C. arnoldii*, which exhibit some evidence of a heterogeneous pit membrane, not only are characterized by circular apertures, but also are the largest pits known within the

[5] We are unaware of published quantitative documentation that supports this proposed correlation. It is probably significant, however, that data we have collected from the literature show, among 57 species of gymnosperms with a torus, a mean pit diameter of 16.0 μm (range 7–26 μm). This contrasts with a mean pit diameter of 11.7 μm (range 7–21 μm) for pits of 16 species of gymnosperms lacking a clearly defined torus. Whereas these data are entirely consistent with a correlation between large pit size and the presence of a torus, as suggested by Jeffrey (1917), a comprehensive original study utilizing modern statistical methods, including, especially, much larger sample sizes, is required for positive confirmation.

genus (Beck, 1962b) with a mean diameter of 16.6 μm. In other species, mean pit diameter ranges from about 10 μm in our fusinized *Callixylon* sp. and *C. newberryi* to 14 μm in *C. erianum*.

We believe it possible, therefore, that the torus had evolved by Lower Mississippian times in *Callixylon arnoldii*. This, of course, is a tentative conclusion based on circumstantial evidence. A positive conclusion must await discovery of this species preserved in a different mode.

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